

THE GENETIC APPROACH TO PROBLEMS OF RARE AND ENDEMIC SPECIES

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One of the questions that every field botanist with an inquiring mind is bound to ask is: Why are some plant species widespread and common, while others are rare and local? The problem of rare species has a twofold fascination; their discovery never fails to provide a thrill, while the analysis of their affinities and distribution often gives valuable clues to the history of floras. It is natural, therefore, that many botanists have given their answer to this question, and that these answers have been as diverse as are the minds of their proponents. Among these answers there have recently appeared a series which has emphasized the genetic constitution of the species involved. The object of the present article is to review the available evidence upon which these concepts are based, to suggest ways in which new experimental evidence for them may be obtained, and to follow out some of their implications when applied to problems of the history of floras and plant evolution.

The word "rare" may not always mean the same thing. Some plants are regarded as rare because throughout a large part of their range they are found only as scattered individuals or small groups, separated by miles from their nearest neighbors. Such is the case with many species of orchids, such as *Calypso bulbosa* (L.) Oakes, *Cephalanthera Austinae* (Gray) Hel., *Cypripedium arietinum* R. Br. and *Aplectrum hyemale* (Muhl.) Torr. In most of these cases, however, there are some regions where the species concerned are abundant. *Calypso*, for instance, is common enough in the northern Rocky Mountains, as is *Cypripedium arietinum* in parts of southern Ontario, while the rarity of *Aplectrum* is due largely to extermination by man. Another type of rarity is extreme localization. A species may occur in only a few widely separated localities, but may be abundant enough where it is found. This is notably true of *Phyllitis Scolopendrium* (L.) Newm. var. *americana* Fernald, the hart's tongue fern in eastern North America. Many species of serpentine barrens in California, such as *Cupressus* spp. and *Streptanthus* spp. are similarly distributed. Still a third type of rareness is extreme endemism. A species may occur only in one or two spots on the entire globe, but in this case it is almost always represented in these spots by hundreds of individuals. These three types are, of course, connected by innumerable intermediate cases. In the writer's opinion, the concepts set forth below will apply with modifications to all of them.

As a necessary background for this study, let us review briefly the most widely current answers to this question of why certain

species are rare. Perhaps the most direct and simple answer is that of Willis (34, 35), who maintains that in general rare and endemic species are beginners, which have not yet had time to spread. The weaknesses and fallacies of this hypothesis have been fully exposed by Fernald (16), Wright (38), and Hubbs (23), so that they need not be dwelt upon here. It will be pointed out below that our present concepts of the genetic structure of species, which have been developed as a result of many painstaking experiments, throw into glaring relief the fallacies of Willis's reasoning. In addition, recent paleobotanical research has added greatly to the number of rare modern species whose fossil ancestors are known to have been common and widespread, and this is particularly true of the endemics of the California flora (Chaney, 7, Axelrod 2, 3).

A second answer was given by Fernald (15, 17, 18), as a result of his keen observations in the field and his careful analysis of the distribution of many rare species in the flora of eastern North America. This is the concept of senescence; that most rare species were once common, but that their great age and the vicissitudes to which they have been subjected have made them "conservatives," and unable to spread. This concept, based as it is upon extensive observations of rare plants as they actually grow in the field, has much to recommend it. Most field botanists will agree with Professor Fernald that conservatism rather than aggressiveness is characteristic of rare plants. In fact, the genetic concept to be reviewed below is based primarily upon this assumption. The weakness, however, of the concept of senescence is the implication that conservatism results directly from the age of a species. There are two large objections to this implication. In the first place a number of species, such as *Sassafras variifolium* (Salisb.) Ktze. *Liquidambar styraciflua* L. and *Ulmus americana* L. are known to have close relatives that go far back into the fossil record, and yet the present species are still widespread and common, having invaded much of the region that was covered by the Pleistocene ice sheet. The other, and perhaps more serious objection is that the same species may be rare and conservative in one part of its range and common and aggressive in another. *Erigeron compositus* Pursh is cited by Fernald (15) as one of the "senescent" species composing the relict flora of the Gaspé Peninsula. In the Sierra Nevada of California, and presumably also in the Rocky Mountains, this species is far from conservative. The variety of habitats which it occupies is matched by the morphological variability of the species itself. *Adenocaulon bicolor* Hook. was considered a "senescent" species (Fernald 18) on the basis of the disrupted range and obvious great age of the genus and the rarity of *A. bicolor* in the Great Lakes region. In California this species grows under redwoods, as Fernald has pointed out, but it is also common under *Pseudotsuga*, *Abies*, *Pinus ponderosa* and other conifers. In the Sierra

Nevada at middle altitudes, however, *Adenocaulon* is far from conservative. It is one of the commonest and most aggressive weeds about cabins, being often the first species to occupy disturbed ground, if sufficiently shaded. From the hypothesis of senescence one would be forced to conclude that *Erigeron compositus*, *Adenocaulon bicolor*, and similar species are old in the east and young in the west. This conclusion seems illogical in the extreme. And in one genus, *Antennaria*, there is direct evidence that the conservative, "senescent" species of the Gulf of St. Lawrence area are actually younger than their common, widespread western relatives. With one exception these Gaspé and Newfoundland antennarias are exclusively apomictic; staminate plants are unknown in them. They therefore are "dead ends" from an evolutionary point of view, and must have originated from sexually reproducing species (cf. Stebbins, 29). Their only close sexual relatives, and therefore their presumable ancestors (*A. umbrinella* Rydb., *A. microphylla* Rydb., *A. reflexa* Nels., *A. media* Greene, *A. monocephala* T. & G., etc.) all occur in western North America, and are for the most part widespread, common, and aggressive enough to have colonized extensively areas vacated by the Pleistocene glaciers. Therefore, the conservatism of the relict *Antennaria* species cannot be due to age alone, since their ancestors have still retained "youthful" characteristics.

The third answer to this problem of rare species is the genetic concept which is to be reviewed in the present paper. It is based upon the realization, as a result of the experiments of Turesson and others (cf. Turesson, 31; Hiesey, 22; Clausen, Keck and Hiesey, 8), that most widespread and common plant species consist of a large number of genetically different biotypes, many of which differ widely in their ecological preferences. This is, of course, the basis of the ecotype concept, which conceives of these widespread species as consisting of several clusters of similar biotypes, each cluster, or ecotype differing from other ecotypes in its ecological preferences. On the basis of this concept, the range of ecological tolerance of a species, in the sense of Good (20), embraces the tolerance ranges of all of its component ecotypes and biotypes. Naturally, therefore, a species with many ecotypes and biotypes will be widespread and common. And conversely, a species which is poor in biotypes, and has only one ecotype, will be rare, unless its individual biotypes have a wide range of ecological tolerance, or unless the particular conditions to which they are adapted are widespread. A rare species, therefore, may be conceived of in genetic terms as one poor in biotypes, and with its biotypes so specialized that they can grow and compete with other species in only a limited area. Aggressiveness, or the ability of a species to colonize new areas, and to crowd out other species, is the result of the possession of a great store of genetic variability either evident or concealed. This consists of genetic heterozygosity, of biotypes preadapted to new conditions

which the species might encounter, or of a rapid mutation rate, by which new biotypes may be produced. A species is conservative, on the other hand, if it contains few biotypes, most of which are homozygous or nearly so, and has a low mutation rate.

This concept was foreshadowed by Darwin's classic statement that "wide ranging, much diffused, and common species, vary most." It was hinted at some time ago by Turesson (31), but so far as this writer is aware was first clearly stated by Anderson (1, p. 496). Hultén (24) made it the cornerstone of his brilliant analysis of the history of the Arctic flora, while Camp (6) used it to explain the relative constancy and limited distribution of some species of the interesting genus *Befaria*. Cain (5) pointed out the advantages of this concept over that of senescence, while Raup (28) recognized it as an important factor in the distribution of species of boreal America. Fassett (14) made the determination of genetic constancy in certain areas a major objective of his interesting and valuable study of variation in *Rubus parviflorus*.

The main difference between this genetic concept and that of senescence is that it aims to interpret the rarity of species primarily as a result of their present constitution, without implying anything about the past history or future fate of the species concerned. Many, and perhaps most rare species were once more common and aggressive, but not all. The phenomenon of insular species, many of which have always been rare, will be discussed below. The rare conservative species which were once common have been characterized by Turesson (31) and Hultén (24) as having been "depauperated with regard to their biotype contents" (Turesson 31, p. 97). Since the word depauperate is generally applied to plants of small size, its use in the present sense seems inadvisable. The word depleted expresses the situation more precisely and has no other connotation. To those who accept this genetic hypothesis, therefore, the writer suggests that the term "depleted" be used for those rare, conservative species which appear to have been formerly more common and aggressive; i.e., the "senescent" species of other authors.

Griggs (21) has recently sought to explain the rarity of plant species on the basis of competition. He states that (p. 592) "a species is rare because it cannot compete successfully with the common plants," and that "most rare species find their habitats in the early stages of the ecological succession." These statements are supported by a wealth of evidence derived from a study of rare plants in eastern North America. They lead to a conclusion similar to that implied by the term senescence, namely that those rare species which have ranges at present disrupted, but formerly continuous, "are therefore slowly dying out." On the basis of this hypothesis Griggs admittedly has difficulty in explaining the fact that many of the plants which are rare in eastern North America are common in the west. And if one examines the plants which are rare in western America, particularly those of

California, one finds that Griggs' hypothesis does not apply to a large number of them. The most famous rare species in California is the big tree, *Sequoiadendron giganteum* (Lindl.) Buchholz. Others, almost equally famous to botanists, are *Cupressus macrocarpa*, *Pinus Torreyana* Parry and *P. radiata* Don, *Picea Breweriana* Wats., *Abies venusta* (Dougl.) Koch, *Quercus Sadleriana* R. Br., *Crossosoma californicum* Nutt. and *Lyonothamnus floribundus* Gray. None of these species can be said to "find their habitats in the early stages of ecological succession." They are sub-climax, climax, or post-climax types. Furthermore, such observations as have been made indicate that in restricted areas and under certain conditions these species can compete very well with their common associates. Mr. Woodbridge Metcalf of the Division of Forestry, University of California (unpubl. bulletins and oral comm.), has found that seedlings of the big-tree may under certain conditions become established in great numbers. Once established, they grow very rapidly and in one forest, started through natural re-seeding in the early eighties, "none of the associated species have been able to keep pace with the sequoias in height, though there are some excellent specimens of sugar pine, *Pinus Lambertiana*, and white fir, *Abies concolor*, in situations where they have not been too much crowded by the big-trees." Apparently the limits to the spread of this most famous of rare plants, are the specialized conditions necessary for the successful establishment of seedlings. These are chiefly a disturbed mineral soil, and a sufficiently early onset of the fall rains during the early years of growth. In these respects the seedlings of the common species of Sierran trees are much less particular. Another rare Californian, *Pinus radiata*, the Monterey pine, is a very good competitor in the regions where it grows naturally. Last spring the writer led a class through a clearing in a grove at the northernmost of its three natural localities, Ano Nuevo Point. Although this clearing had gone over completely to grassland (the predominant plant formation for miles along the coast both north and south of the four mile stretch of pine forest) it was filled with vigorously growing pine seedlings, which will soon crowd out the grass, and restore the area to its natural cover of pines. Furthermore, there were abundant seedlings of *P. radiata* throughout the stand, and in some places beyond its edges, so that one could not possibly draw the inference that the species is dying out. Mr. H. A. Jensen, of the California Forest Experiment Station has informed the writer that the southernmost grove of *P. radiata*, at Cambria, was once extensively lumbered, and has since restored itself. Hence neither the statement that rare species occupy chiefly pioneer habitats nor that they are slowly dying out applies to the most famous of Californian rarities.

Griggs' hypothesis, however, still is of great value in interpreting many of the rare plants of eastern North America. Furthermore his emphasis upon ability to compete as a major

factor in the distribution of both rare and common plants is fully justified and is an important part of the concept of genetic homogeneity as here presented. This seems evident from the writer's preliminary observations of one of the most interesting endemics of the San Francisco Bay region, *Dirca occidentalis* Gray. This species is restricted to an area about ninety miles long and twelve miles broad, being most abundant in the Oakland and Berkeley hills. Its nearest relative, which it resembles rather closely, is the wide-spread eastern American *D. palustris* L. (fig. 1). In contrast to the swamp habitat of the eastern species, *D. occidentalis* occurs principally upon well-drained hill slopes, where its chief competitors are other shrubs, such as *Toxicodendron diversilobum*

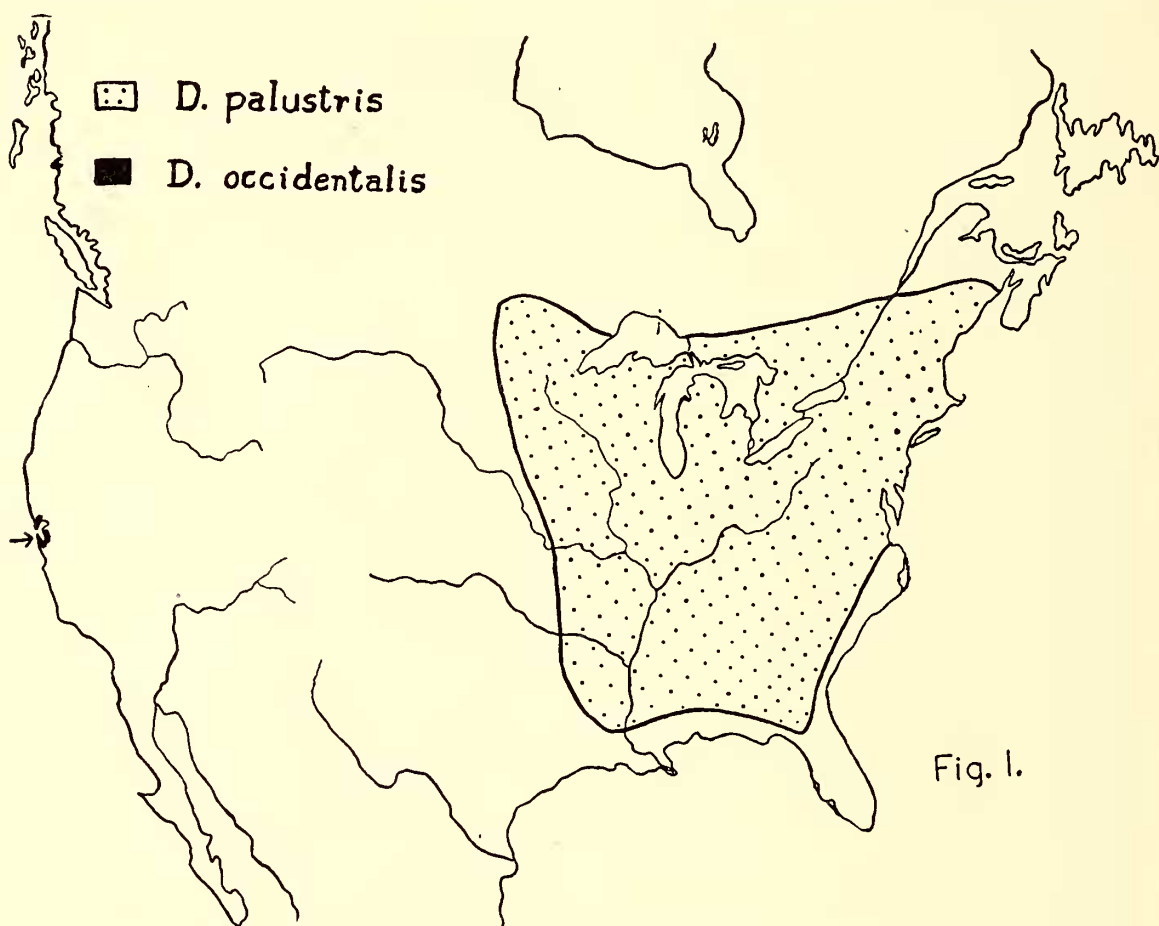


FIG. 1. Ranges of *Dirca palustris* and *D. occidentalis*.

(T. & G.) Greene, *Baccharis pilularis* DC., *Rhamnus californica* Esch., and *Osmaronia cerasiformis* (T. & G.) Greene. In Wildcat Canyon, just east of Berkeley and still within the summer fog belt, *Dirca* is rather common, and in a few places forms almost pure stands. Here the writer has observed several clearings in sheltered north and east facing slopes, where *Dirca* seedlings were more abundant than those of any other shrubs, and were competing on equal terms with *Toxicodendron*, and doing better than *Baccharis* or *Rhamnus*. On such slopes young *Dirca* seedlings can be found everywhere under the other shrubs, so that there seems no more reason to suppose that it is dying out than that *Rhamnus*, *Osmaronia*, or *Symphoricarpus albus* are disappearing from this

area. On the sunnier west and south facing slopes, however, adult *Dirca* shrubs are sometimes found, but no seedlings have been observed. *Toxicodendron* and *Baccharis*, on the other hand, are equally vigorous and self-perpetuating in both sites. If one travels two miles east from Wildcat Canyon, crossing a ridge 1500–2000 feet high, one reaches the inner edge of the fog belt, where the summer weather is considerably drier and hotter. Here *Dirca* is rather local, and occurs only in shade. The only extensive stand seen by the writer was in dense shade under a grove of live oaks (*Quercus agrifolia* Nee), a habitat which it never occupies in Wildcat Canyon. Here it was accompanied, as usual,

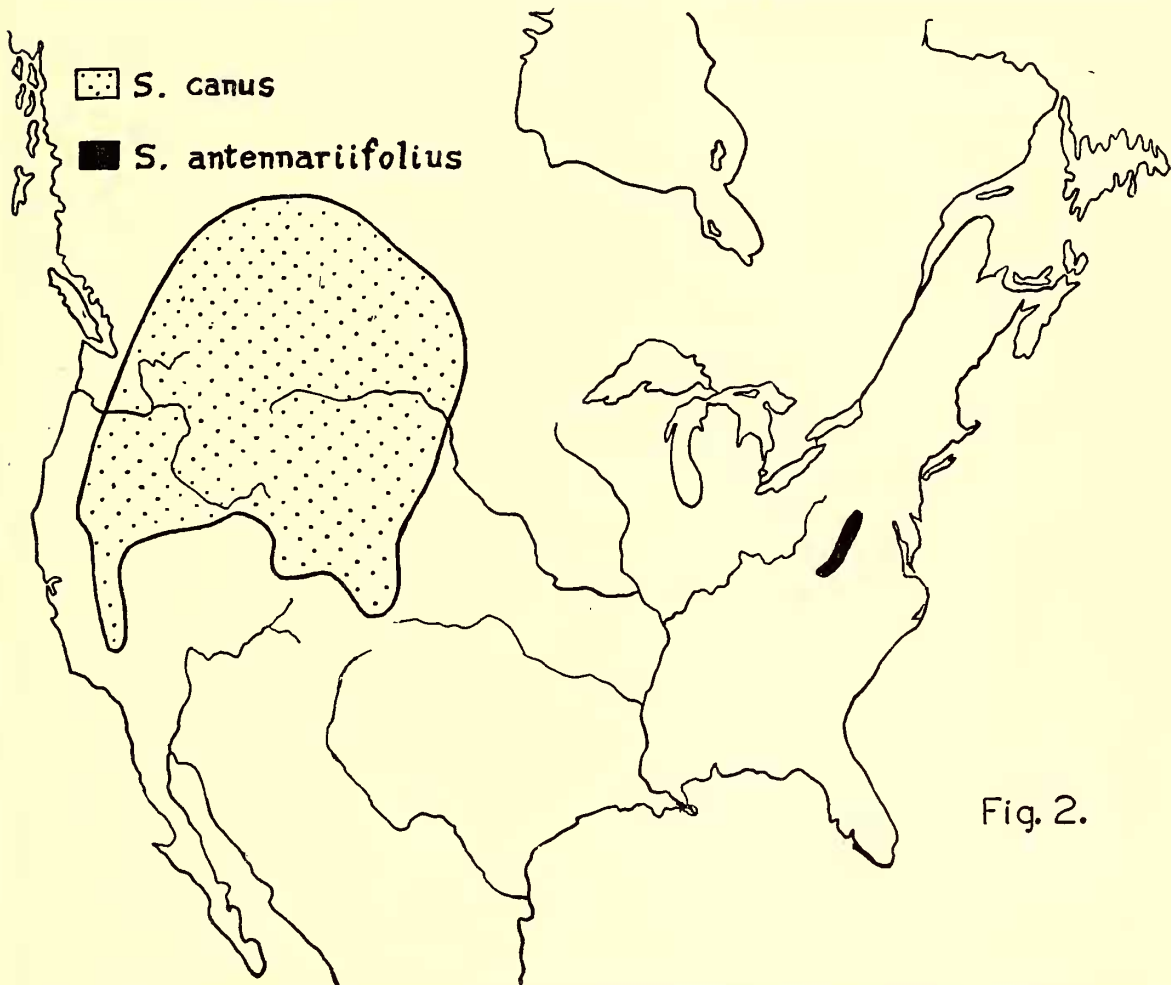


Fig. 2.

FIG. 2. Ranges (generalized) of *Senecio canus* (*sens. lat.*) and *S. antennariifolius*.

by poison oak (*Toxicodendron*), but the latter species was also abundant on the open, sunny slopes away from the oaks. Going eastward from Orinda, one would have to travel 1500 miles before he would see *Dirca* again. The logical inference from these observations is that *D. occidentalis* contains only a few biotypes, with a limited range of tolerance. These are successful only in sheltered spots, and may require the rather heavy type of soil characteristic of the Berkeley Hills. In the fog belt, they are only moderately tolerant of shade, while in the warmer regions east of the fog the seedlings can compete successfully only in deep shade, where they are met and surpassed by the more vigorous

competition of such undershrubs as *Rhus*, *Osmaronia*, *Symphoricarpos albus* (L.) Blake and *Corylus rostrata* Ait. var. *californica* A. DC. These more common competitors, on the other hand, appear to possess biotypes which can withstand a variety of sun and shade conditions in both Wildcat Canyon and Orinda.

The above argument may be summed up by a definition of the concept of *genetic homogeneity*, as follows. In continental areas, most rare or narrowly endemic species are genetically homogeneous, and may therefore be termed *homogenic*. They consist of relatively few biotypes which are themselves relatively homozygous. In contrast, the common and widespread species are usually heterogeneous in their genetic makeup. They include many biotypes, often grouped into more or less distinct ecotypes, and a large proportion of their individuals are genetically heterozygous, possessing a store of genetic variability beyond that which is evident from the appearance of their phenotypes.

This concept of genetic homogeneity, however plausible it may seem, is nevertheless only a working hypothesis. It should be put to the acid test of experimentation. Two lines of attack occur to the writer. In the first place, the genetic variability of typical rare species should be tested by growing under constant, controlled conditions progenies from all parts of their ranges. This variability should then be compared with that found in a series of progenies of their most common competitors, taken from various parts of the range of the rare species, as well as from beyond that range. Finally, in the case of species that are rare in one part of their range and common in another, or of those rare species that have close relatives elsewhere it should be possible to inject new variability, and therefore new aggressiveness into them by means of hybridization. In other words, if the concept of genetic homogeneity as the cause of "conservatism" is valid, wide intervarietal or interspecific crossing should replenish the biotype supply, and make for increased aggressiveness. Some of the new hybrid derivatives should then be easier to establish in new sites than the original rare species.

While recognizing that this hypothesis needs experimental confirmation, we can nevertheless follow out some of its implications. In the first place, it is entirely incompatible with the hypothesis of "Age and Area." The concept of genetic homogeneity is based partly on the assumption that in terms of the geological time-scale the migration of young species into new territory is rapid or at least fast enough to keep up pretty nearly with the prevailing rates of climatic change. The distribution of a species will be a reflection of its store of genetic variability only if each ecotype can occupy all of the contiguous territory to which it is suited in a relatively short period of time. This assumption, diametrically opposed to Age and Area, was emphasized by Gleason (19) and explains the facts of distribution as the present writer has observed them. Many species whose seeds have no

obvious means of rapid dispersal are widespread in new territory. The lupines of California are good examples. On the other hand, many species with apparently excellent means for dispersal are highly restricted. To cite just one instance, there are in California a number of native species of thistle (*Cirsium*), all with presumably equally efficient methods of seed dispersal. Some of these, *Cirsium fontinale* (Greene) Jepson, *C. campylon* Sharsmith, *C. Andrewsii* (Gray) Jepson, and *C. Vaseyi* (Gray) Jepson are more or less rare and local. One cannot ascribe this localization to the recent origin of the forms in question and the consequent lack of time for their distribution, since various European thistles, such as *Cirsium lanceolatum* (L.) Scop., *C. arvense* Scop., and *Silybum marianum* Gaertn., with apparently no better methods of seed dispersal than the native species mentioned, have become common in various parts of California within the past hundred years or less. These rare California thistles have failed to spread because they are not adapted to any of the areas adjoining their present ranges.

Furthermore, the genetic concept of intraspecific variability offers an entirely different, and in the writer's opinion more satisfactory, explanation of the facts upon which Willis has based his hypothesis. Willis's two main lines of evidence are first that endemic species are in general rarer even in the places where they occur than are widespread species in the same area, and second that the ranges of related species often overlap in "chain-mail" fashion, so that at the limits of their ranges they may intermingle with each other. The first point, which is borne out by most rare species, is entirely compatible with the concept of the genetic uniformity of rare species. These species are adapted to only a few ecological niches, and these niches are not only restricted geographically, but are in general of small extent even in the regions where they do occur. To use a simile: a physician belongs to a widespread and common profession. Not only is there room for physicians in every town in the world, but in addition a city can absorb a large number. A botanist, on the other hand, belong to a profession which is rare and local. There are only a few cities, those which possess a large institution of learning, in which a professional botanist can survive at all, and in these botanists are much rarer than physicians, because there are many fewer places which they can occupy. Similarly a plant species with a narrow range of tolerance will tend to be not only localized geographically but also rare where it does occur.

The "chain-mail" pattern of distribution can be explained equally well upon the genetic concept, without resorting to "Age and Area." Willis argues that if two related species are found together in the same forest one cannot assume that they have different ecological preferences. This may be in part true, although one cannot help remarking that every forest or meadow has inequalities, however slight, of topography, exposure, soil,

moisture, etc., which would permit individuals with unquestionably different ecological preferences to grow near each other. But even if we grant that two groups of individuals belonging to different species have the same genetically conditioned ecological requirements, we need not conclude from this fact that the two species as wholes have the same range of tolerance. The biotypes which are ecologically equivalent may represent opposite extremes of the ranges of genetic variability of the two species. The normal or average biotypes of the two species may be very different from each other. For instance, *Pinus ponderosa* (*sens. lat.*) and *P. contorta* var. *Murrayana* overlap in the Sierra Nevada in typical "chain-mail" fashion, so that forests exist where the two species grow side by side, although in general *P. ponderosa* grows at lower altitudes and in drier situations than *P. contorta* var. *Murrayana*. This overlapping may mean that the hardest, most moisture tolerant individual biotypes of *P. ponderosa* are nearly or quite equivalent to the least hardy, most drouth resistant ones of *P. contorta* var. *Murrayana*, but it certainly does not mean that the two species as wholes are ecologically equivalent. In fact, the only reasonable conclusion which one can draw from the ranges of these two species, which occur separately over enormous stretches of territory, at very different altitudes and latitudes from each other, is that they have very different ranges of tolerance. And there is no case of "chain-mail" distribution known to the writer to which the same explanation cannot be applied.

When "Age and Area" has been eliminated, there remain two possible conditions of the past history of a rare species. One is that the species was once more common, widespread, and richer in biotypes than now, so that its present rarity is due to depletion of the store of genetic variability. The other is that the species never was common, but diverged from a small group of individuals of a widespread ancestral species, following the establishment of these individuals upon a small insular area. There are thus two types of homogenic rare species, *depleted species* and *insular species*.

The evidence from both paleontology and present distribution indicates that depleted species are frequent, and constitute a large proportion if not a majority of rare species (Fernald, 16, Axelrod, 2). The process of depletion has two stages. First, the widespread, common species becomes reduced in geographic distribution and in numbers through climatic or geological changes which eliminate many of its original habitats. During this process many biotypes and ecotypes are automatically destroyed, both through the complete elimination of the species from many areas and through more rigid selection in the few regions where it can survive. After this reduction in numbers, the species may still preserve a considerable amount of individual genetic variability, as well as a store of potential variability in

the form of recessive genes for which the individuals are heterozygous. Its continued existence as a series of small, completely isolated populations will, however, automatically lead to the further depletion of each population. As Wright (37) and Dobzhansky (12, p. 334) have pointed out, such small populations become more uniform genetically on account of inbreeding. Recessive genes tend to express themselves phenotypically, and thus become eliminated through adverse selection. Furthermore, the process known as random fixation takes place, so that purely by the vagaries of chance each population becomes uniform for a series of non-adaptive characteristics which in the larger population varied from individual to individual. This, of course, leads to the divergence of the isolated populations. It explains the fact that depleted species are usually sharply defined, that is morphologically very distinct from their nearest relatives, as well as being relatively uniform.

In addition to the depleted species, there is also a large body of rare species which have always been so because they have never had an opportunity to spread. Since such a condition is most characteristic of islands, rare species of this type can be termed *insular species* (Kinsey, 25). If through some accident a small group of individuals of a continental species becomes established upon an island, they will carry with them only a small part of the genetic variability of the original species. Furthermore, inbreeding and random fixation will tend further to make this insular population more uniform and more different from its continental ancestor as the years of its isolation progress. Thus the genetic structure of a restricted insular species becomes homogenic as does that of a depleted one.

There is, however, one way in which insular populations can maintain a certain degree of variability. If the insular areas are near enough to the continental ones or to other islands so that the migration of individuals to the island can occur repeatedly, the insular population can periodically be enriched with a new infusion of genetic variability. It becomes the semi-isolated population which, according to Wright (37), has the best potentialities for evolutionary progress. If the insular area or areas are small, the species will remain rare, but it will have an unexpected amount of variability. Thus a rare species confined to several small, insular areas partly isolated from each other is an exception to the hypothesis stated above of genetic uniformity for rare species. It has a potential aggressiveness, but cannot spread because it has no place to go.

Insular species are most easily recognized when they occur on actual islands, but they also exist within continental floras. Any species which occurs in a small area of favorable territory surrounded by extensive areas which neither it nor any of its close relatives could possibly occupy is as isolated as if it were on an island (cf. Kinsey, 25). This is true of the species of isolated

mountain tops which contain an alpine flora but are surrounded by great stretches of temperate or tropical lowland; of those found in oases in a desert, whether the oases are associated with streams, springs, or isolated mountain ranges, and of those in many types of habitats which are radically different from their surroundings.

It is on one of these terrestrial "islands" that there occurs the example best known genetically of a plant species which, though rare, has an unexpected amount of variability due to its existence in a series of semi-isolated colonies. This is *Oenothera organensis* Munz (*O. macrosiphon* Wootton & Standley) endemic to the Organ Mountains of New Mexico, which occurs in a series of small colonies along the only living streams found in this arid range of mountains completely surrounded by desert. It is a mesophyte living in the only mesophytic habitats available to it. Emerson (13) found that *O. organensis* has an unexpectedly high number of genes for self-incompatibility. Wright (36) on the basis of his mathematical deductions, could explain this situation only by assuming that the total number of about five hundred individuals found in the species was divided into a series of small, semi-isolated colonies, an assumption fully warranted by its distribution. *Oenothera organensis* may have a good deal of potential aggressiveness, which might result in a spreading of the species if an increasingly moist climate should open up new habitats to it.

In discussing the flora and fauna of actual islands, the distinction is often made between continental islands, which were formerly connected with some large land mass, and oceanic islands, which have never been so connected (Baur, 4). The flora and fauna of the former are said to be harmonious, since they are derived entirely from one continental area, while those of the latter are termed disharmonious, being derived from two or more different continental areas, and by several different migrations from each area at widely separated intervals. Terrestrial insular areas may be similarly classified as to their origin. Many, such as most of the alpine regions in mountain ranges of the north temperate zone, were once connected with extensive continental areas of similar ecological conditions; others were never so connected. The latter nearly always provide striking cases of endemism.

One such area in the eastern United States is the famous series of shale barrens in the Appalachian Mountains, extending from southern Pennsylvania to southwestern Virginia and eastern Tennessee. These barrens occur wherever rocks of certain geological formations outcrop on steep slopes. They are mildly arid as well as poor in mineral matter, so that they support a flora more xerophytic than that in the surrounding hills (Core, 11). Although each slope is obviously a pioneer habitat, destined to disappear as soil accumulates on it, new barrens are constantly being created by weathering and stream erosion, so that the shale barren habitat has probably existed continuously ever since the

uplift of the Appalachians began early in the Tertiary period, and will continue to exist as long as these mountains stand. They thus represent, like the seashore, a "pioneer" habitat of permanent duration, at least so far as present-day species are concerned. Although the climate of the Appalachian region may at times have been drier than it is now (Gleason, 19, Core, 10), there is no reason to believe that it was ever arid or even semi-arid, so that the possibility that the shale barrens were ever joined to the large semi-arid areas in the central and western United States by a continuous stretch of territory similar to the present barrens is rather remote. Hence they represent semi-xerophytic islands in a region dominated by a mesophytic forest. The flora of these shale barrens, as analyzed by Wherry (32, 33), contains species of rather diverse affinities. Some like *Senecio antennariifolius* Britton, are closely related to xerophytic western species. Others, like *Oenothera argillicola* Mackenzie, show certain characteristics in common with western species, but no close relationship. Cleland (9) has pointed out that *O. argillicola* resembles the western *O. Hookeri* alliance in its large flowers, self-incompatibility, and in forming pairs of chromosomes rather than rings at meiosis. In other morphological characteristics, however, it is more like some of the eastern species, and the arrangement of its chromosome segments is somewhat different from that of any other species. Still other shale-barren species, like *Pseudotaenidia montana* Mackenzie, are of very obscure affinities. Finally there is a series of shale barren species which have obviously evolved from mesophytes of the surrounding flora. Some of them are specifically different from their mesophytic relatives, others are apparently only ecotypes, while still others are of doubtful status. In view of this diversity of affinities, the hypothesis of Wherry (32, 33) that all of the shale barren plants originated somewhere to the northwest, seems unlikely. The plant association of these barrens appears rather to have been gradually built up over a long period of time through the addition at widely separated intervals of plants derived from very different sources.

In the west, such permanently isolated areas are more common. The mountain ranges of the southern Great Basin are excellent examples. They were uplifted during the latter part of the Tertiary period (Loudenback, 26), and it is very unlikely that the forest and alpine areas of their higher slopes were ever continuous with those of other mountains. The best known of them floristically is the Charleston Range of southern Nevada. The enthusiastic and thorough explorations of Mr. Ira W. Clokey have uncovered a large number of endemic species of diverse affinities, and the high montane flora as a whole differs from all others in the world.

Another series of examples on a much smaller scale are the serpentine barrens of central California. Species of certain genera, like *Streptanthus*, will grow in this region only on serpen-

tine, so that these barrens for them are and probably have always been islands. Some of these *Streptanthus* species are endemic to only one or two barrens (Morrison, 27). These have probably always been rare, and may have been derived rather recently from the more widespread species by the establishment and divergence of an insular population as described above. So far as the writer is aware, no study of the geographic affinities of the serpentine barren endemics has been attempted; on the basis of the present discussion, these affinities should be diverse.

Not all species now endemic to islands are insular in the sense that their present population has been derived from a few individuals of an existing continental species. Relict, depleted species have been preserved on many islands, as well as on terrestrial insular areas (Baur, 4). This is particularly true of islands of continental derivation, and may be due to the lower intensity of competition as compared with continental areas. The Channel Islands off the coast of southern California, for instance, have preserved the last remnants of such species as *Lyonothamnus floribundus* Gray, *Prunus Lyoni* (Eastw.) Sarg. and *Quercus tomentella* Engelm., which are known through fossil evidence to have been formerly more widespread, and very likely consisted of several ecotypes (Axelrod, 2, 3). Even on oceanic islands or those with remote continental connections there are often found species which are apparently either the last relics or the immediate derivatives of ancient genera now extinct elsewhere. This is well illustrated by some of the arboreal Compositae of the Pacific Basin. Two of the archipelagoes west of South America, namely Juan Fernandez and the islands of San Felix and San Ambrosio contain endemic genera of the tribe Cichorieae; *Dendroseris* on Juan Fernandez and *Thamnosseris* on San Felix and San Ambrosio, which are related neither to each other nor to any other genus found in the Southern Hemisphere. *Thamnosseris* appears to be nearest to *Stephanomeria* of western North America, particularly *S. Blairii* Munz & Johnston, an anomalous endemic of San Clemente, one of the Channel Islands. *Dendroseris* is of more obscure affinities but is also most nearly related to North American genera. The modern species of both *Thamnosseris* and *Dendroseris* therefore, must have had more widespread ancestors, and are to be considered as relict, depleted genera. Another case is *Hesperomania*, endemic to Hawaii, where it is very rare. Its nearest relatives are *Augusta* (*Stiffia*) of Brazil and *Nouelia* of southwestern China. All three are apparently the last remnants of a group which must have been widespread in the Northern Hemisphere in Cretaceous or early Tertiary time (Stebbins 30). *Fitchia*, endemic to two islands of Polynesia, is an extraordinary genus which combines the characteristics of the tribes Mutiseae, Heliantheae, and Cichorieae, but has no close relatives in any of them. It is obviously a relict genus, perhaps a survivor of an ancient stock of

Compositae which existed before the present tribes became differentiated from each other.

Since both insular and depleted species may occur on insular areas, terrestrial as well as actual islands, the differentiation between the two types in such areas is a difficult problem. No set rule will hold for all species, but two criteria can be considered as valuable. First, if the endemic is closely related to a widespread species which occurs on an adjacent continental area, it is probably a strictly insular species, while if it is closely related to no other living form, or has its relatives in some remote corner of the globe, it is more likely a depleted species or a derivative of one. Second, if the endemic is morphologically a highly specialized type in relation to its continental relatives, it is probably an insular descendant of these; while if it is less specialized it may be their depleted ancestor.

Finally we must consider the future of these homogenic rare species. The most obvious fact is that they are more at the mercy of climatic changes than are the common, variable species. Just as their genetic rigidity prevents them from occupying new habitats, so it must also reduce their power to adapt themselves to climatic changes. Hence if the climate remains the same they may persist as rare species indefinitely. If it becomes more unfavorable to them, they are likely to disappear. This is the fate awaiting many Californian trees and shrubs, notably *Pinus Torreyana*, *P. radiata*, *Abies venusta* and *Cupressus macrocarpa*, if the progressive desiccation of our climate continues. On the other hand, if conditions become more favorable for the spread of their few remaining biotypes, they may become more common. Then, if two or more isolated colonies of a depleted species are enabled to spread until they meet, a partial replenishment of the store of genetic variability may take place. During their isolation the disjunct colonies must have acquired some different genetic characteristics, both by mutation and by random fixation (Wright, 37, Dobzhansky, 12). Thus when two such colonies reunite, hybridization between genetically different individuals is made possible. By this means, a large number of new genetic combinations may arise, replenishing the store of genetic variability, and opening up new possibilities for the spread of the species.

Examples of species that have apparently been replenished in this fashion are provided by relatively widespread and common members of mono- or ditypic genera which occur in the same region and appear to be somewhat related to each other, but are very sharply set off morphologically and have no close interrelationships. Such a group is found among the Compositae, tribe Cichorieae of the Sonoran desert of western North America. Here there are two monotypic genera, *Anisocoma* and *Atrichoseris*, and three ditypic ones, *Rafinesquia*, *Calycoseris*, and *Glyptopleura*. These are all related to each other and to the larger genera *Stephanomeria* and *Malacothrix*. Together with *Pinaropappus* of

Texas and Mexico as well as the insular *Thamnosseris* mentioned above, they form a natural group, not closely related to any other Cichorieae. The small size and remarkable distinctness of the genera and most of the species of this group is in sharp contrast to the situation in the Cichorieae of the Old World, where most of the genera are relatively large and are so closely interrelated that generic boundaries are very difficult to define. Supposing, however, one were to select a dozen species from each of the large Old World genera *Lactuca* and *Crepis*, and one or two each of *Hypochaeris*, *Leontodon*, *Sonchus*, *Launea*, *Ixeris*, and *Youngia*, choosing the more xerophytic members of each genus and should then deposit these species upon a semi-arid or desert area completely devoid of Cichorieae, and they all became established in this area, the resultant pattern of variation would closely simulate that now found in the western American Cichorieae mentioned above. This suggests the hypothesis that exactly such a process of selection has taken place in the history of the latter. Their history may have been somewhat as follows. Once the entire group consisted of a few fairly large closely interrelated genera, or of one genus divided into several sections. Then the group became much reduced in numbers, due to the reduction in extent of the habitats which it occupied, and was broken up into many partly or completely isolated populations. The larger of these retained their store of genetic variability throughout the period of reduction. The smaller ones, being subject to intense selection and random fixation diverged sharply from the ancestral stock, and at the same time became much depleted genetically. Then with the restoration of conditions favorable to the group, all of the remaining species were able to spread again. Those less completely isolated then gave rise to the more closely interrelated species of the larger genera *Stephanomeria* and *Malacothrix*, while the descendants of the strongly isolated and depleted small populations became the distinctive mono- and ditypic genera. This history may be greatly oversimplified; perhaps several cycles of depletion and replenishment were necessary to produce the pattern of variation found in this group. Nevertheless, the occurrence of such cycles in the evolutionary history of this and other groups is a very likely possibility, and may have been of considerable importance in the differentiation of species and genera throughout the plant kingdom.

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SUMMARY

The concept of age and area and that of senescence of species in the stricter sense is not considered adequate to explain the occurrence of rare and endemic species. Instead the writer regards as most important the concept of genetic homogeneity.

This assumes that most common and widespread species are genetically diverse, while rare and endemic ones contain relatively little genetic variability, that is relatively few biotypes. They are therefore termed homogenic. This homogeneity reduces the number of ecological niches in which the rare species can compete successfully with other species, but if the climate is a stable one, does not necessarily cause their extinction. From the historical point of view there are two types of homogenic species. Depleted species are those which formerly were widespread and genetically diverse, but have lost many or most of their biotypes. A species may become depleted in only one part of its range, remaining common and variable in another. Insular species are those which have developed on an island or an isolated ecological habitat on a continent. They have originated from a few individuals or a single individual of the ancestral species, and have never possessed great genetic variability. The distinction between depleted and insular species is often hard to recognize, because depleted species often find their last refuges in insular areas. The future of rare, homogenic species depends upon the future of the ecological niches to which they are adapted. If the environment remains stable, they can persist indefinitely as rare species. If changes occur which obliterate their restricted habitats, they will become extinct. If, however, environmental changes result in an increase of the particular ecological conditions to which the species is adapted, it can spread. Then if this spreading permits the coming together of two isolated colonies of a homogenic species or of two such species which are still capable of interchanging genes, the populations thus united will both acquire new genetic variability. By this means a homogenic species may become diverse and widespread. If it is a depleted species, part or all of its original diversity may be restored.

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